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The chemical ecology of herbivory on willows

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Synopsis

Phenolic secondary compounds and trichomes are instrumental in the regulation of herbivory on Salicaceae. The roles of phenolics in willows as toxins or deterrents, as phagostimulants or ovipository signals, and as precursors in insect chemical defence are briefly reviewed. The interactions between salicaceous plants, herbivores and their predators are discussed in the context of theories on the evolution of interactions among three trophic levels.

Introduction

Plant secondary metabolites have direct and indirect influences on herbivores by acting as toxins or by triggering various components of their feeding and reproductive behaviours, and by affecting their natural enemies. Secondary metabolites of Salicaceae are mainly phenolics, e.g. phenolglucosides, flavonoids and tannins (Hegnauer 1973; Palo 1984). We outline here how these phenolics regulate herbivory on salicaceous plants, putting the emphasis on the interactions between willows, leaf beetles and their predators. We then discuss secondary chemistry of willows in the light of recent theories on the evolution of plant defence and plant/insect interaction.

Phenolics and plant defence against herbivores

The Salicaceae are characterised by the presence of phenolglucosides in their tissues. Some of these compounds are indeed used as taxonomic markers (Julkunen-Tiitto 1986). The mixture of compounds present can be species specific and within a salicaceous species they can also be tissue specific (e.g. difference between barks and leaves, Palo 1984). Salicin and other phenolglucosides such as salicortin, populin or tremulacin are typically encountered in the northern temperate Salicaceae.

Northern temperate willows can be broadly separated into two groups: those with rather glabrous leaves, rich in phenolglucosides but with low contents of other types of phenolic compounds such as condensed tannins (e.g. *S. fragilis* L., *S. nigricans* Sm., *S. purpurea* L., *S. babylonica* L.) and those whose leaves are densely covered

with trichomes on their undersurfaces, and in which the leaf content of phenolglucosides is low but that of other phenols high (e.g. *S. alba* L., *S. caprea* L., *S. cinerea* L.) (Hegnauer 1973; Rowell-Rahier 1984a). In all species phenolglucosides are present in the bark.

Strong quantitative differences are observed between individuals of the same species (e.g. between clones of *S. orestera* C. K. Schneid, Smiley *et al.* 1985), and of course between different hybrids of the same parent species, *S. fragilis* × *alba* (Soetens *et al.* 1991). Some individual intraspecific variations can be linked with growing conditions. Both fertilisation and shade reduce the phenolic content of twigs of *S. alaxensis* Coville. Twig phenolics are positively correlated with carbohydrate resource (Bryant 1987). Increasing light intensity in combination with low nutrient conditions results in leaves of *S. dasyclados* Wimm. with higher phenolic content (Larsson *et al.* 1986). Similarly, Price *et al.* (1989) show a positive correlation between phenolglucosides concentration and shoot length in *S. lasiolepis* Benth. under high-carbon/low-nutrient growing conditions, but the correlation became negative when the nutrient stress was removed with fertiliser. In this willow, phenolic and protein contents of the leaves are inversely correlated (Waring & Price 1988).

Within a salicaceous species, the phenolic content of both bark and leaves can vary temporally (e.g. in young and mature leaves) (Thieme 1965a; Thieme & Benecke 1971; Hegnauer 1973; Palo 1984). The phenolic content of the leaves is usually higher in spring than in late summer (Thieme 1965a; Rowell-Rahier 1984c; Lindroth *et al.* 1987). However, in tundra and boreal forest, i.e. under poor growing conditions, willows are more palatable in the spring, suggesting for that season a lack of defence and a maximum investment in growth (Bryant *et al.* 1983).

In some willow species sexual differences are also observed, males having lower levels of phenolglucosides than females (Thieme 1965b; Price *et al.* 1989).

Phenolics can be both toxic and deterrent to herbivores. Salicylic acid, the active metabolite of salicin, is well known in pharmacology. At an ecological level, phenolglucosides inhibit the feeding of some vertebrates, for example the mountain hare (*Lepus timidus* L.) (Tahvanainen *et al.* 1985a) and the opossum (*Trichosurus vulpecula* (Kerr)) (Edwards 1978). Internodes of the balsam poplar (*Populus balsamifera* L.) are unpalatable to snowshoe hares (*Lepus americanus* Erxleben) because of their content of either salicaldehyde (in juvenile internodes) or 6-hydroxy-2-cyclohexone (= 6-HCH) (in current annual growth); both these compounds originate from enzymatic conversion of phenolglucosides. Several phenolglucosides metabolites have antimicrobial actions and these can be detrimental to animals relying on symbiosis with microbes for digestion and vitamin production (Reichardt *et al.* 1990). Boreal populations of *Salix* species have a strongly female biased sex ratio. This is due to differential vole winter herbivory, male willows being more palatable than females, possibly because they contain less phenolics than females in their bark (Elmqvist *et al.* 1988).

Several recent studies also identify phenolglucosides as harmful to herbivorous insects. A thorough investigation of the adverse effects of phenolglucosides on lepidopteran larvae show that enzymatic transformation of these compounds in the gut of the insects is critical in determining their toxicity (Lindroth *et al.* 1988). Cyclohexane saligenin ester resulting from the degradation of salicortin and tremulacin causes gut lesions (Lindroth *et al.* 1988). Degradation is linked to both

β-glucosidase and carboxylesterase activity; to avoid toxicity, the insects should have little β-glucosidase activity and a very efficient carboxylesterase detoxication system (Lindroth *et al.* 1988). This seems to be the case in the specialised, and therefore adapted, *Papilio glaucus canadensis* R. & J., feeding on quaking aspen leaves. *P. g. canadensis* has only one-half to one-third of the midgut β-glucosidase activity of the less adapted, but closely related, *P. g. glaucus* L., which avoids feeding on members of the Salicaceae. Moreover, β-glucosidase activity is suppressed by prior ingestion of phenolglucoside in *P. g. canadensis*, but not in *P. g. glaucus* (Lindroth 1988).

Similarly, Clausen *et al.* (1989) show that salicortin, tremulacin, 6-HCH and its degradation product catechol are toxic to the large aspen tortrix caterpillar (*Choristoneura conflictana* Wlk.) fed on an artificial diet. In the same study, simulated damage to the leaves, and crushing them, induced increases in the concentration of the two phenolglucosides and their conversion in 6-HCH and catechol. This is particularly interesting, since it indicates that phenolglucosides are not only constitutive defence, i.e. present in the plant before attack, but also are induced by damage mimicking insect attack.

Salicin acts on a feeding deterrent receptor of *Manduca sexta* L. (Schoonhoven 1969) and of *Spodoptera exempta* Wlk. (Clark 1981). The larvae of these two species of Lepidoptera normally never come in contact with salicin. Additionally, Lindroth and Peterson (1988) showed that plant phenolglucosides transpose the performance of the southern army worm larvae (*Spodoptera eridiana* (Cramer)). Salicin is also toxic and deterrent for predatory insects such as ants (see below) (Pasteels *et al.* 1986).

In North Wales, female trees of *Salix cinerea* are more numerous than males (Alliende & Harper 1989). Leaves of male trees suffer more damage from predation by insects than those of females or juveniles, and leaves in shaded positions more than those in unshaded positions (Alliende 1989). It is unknown if the extent of leaf damage is related to the phenolic content of the leaves, but it would be worthwhile to investigate this possibility.

Phenolglucosides also have deleterious effects on non-adapted leaf beetles (i.e. those not normally feeding on willows with leaves containing phenolglucosides). In choice experiments with agar-based food with or without addition of salicin, the leaf beetles *Lochmaea capreae* L. and *Gallerucella lineola* L. exhibited the highest amount of feeding on food completely devoid of salicin (Tahvanainen *et al.* 1985b). Salicin is a feeding deterrent for the adults of *Phratora vulgatissima* L. (unpublished results), as is chlorogenic acid for *Lochmaea capreae cribrata* Solosky (Matsuda & Senbo 1986).

In the field, negative correlations between phenolic content and distribution of herbivorous insects have been established and related to interspecific and intraspecific variability in the Salicaceae. For example, the success of the aphid *Pemphigus betae* Doane (a gall inducer) is positively correlated with the size at maturity of the leaves of its host *Populus angustifolia* James, and a strong inverse correlation exists between the concentration of total phenols in a leaf and its suitability for the gall-forming aphid. During the colonisation period, the aphid female is seeking a site with minimal phenol concentration. Further, the females select leaves with a low internal gradient of phenol. This suggests that phenols play a role in microhabitat

selection by a gall-forming aphid (Zucker 1982). In another correlative study involving intraspecific variations in willow phytochemistry, the leaf beetle *Galerucella lineola* fed at a reduced rate on leaves of *S.* × *dasyclados* Wimm. with higher phenolic content (Larsson *et al.* 1986).

It is of course hazardous to draw conclusions solely on the basis of correlative studies, especially when several plant species are concerned, and conflicting results are reported. However, in the laboratory, feeding and/or oviposition preferences have been used to support the hypothesis that willow leaves of high phenolic content are avoided by herbivorous insects and that these compounds have a defensive function for the plant. Indeed, variation in susceptibility of willows to herbivore attack can be identified by different indicators such as change of oviposition preferences, change in feeding behaviour and ensuing damage to the plants, and change in the fitness of the herbivore feeding on the plant.

Denno *et al.* (1990) compared larval performance and oviposition preferences of two leaf beetle species on willows with different phenolglucoside patterns. For one species, *Galerucella lineola*, the results were the same for both sets of indicators. Larval performances were inversely related to phenolglucoside contents of the leaves. For the second species, *Phratora vitellinae* L., larvae developed equally well on leaves of willows poor and rich in phenolglucosides (*S. viminalis* L. and *S. fragilis*), but the females showed a marked oviposition preference for the phenoglucoside-rich willow. The importance of phenolglucosides for the larvae will be discussed below.

In food plant choice experiment, Tahvanainen *et al.* (1985b) found that the leaf beetle *Lochmaea capreae* prefers willows with a moderate to low total concentration of phenolglucosides. Interestingly, *Phratora vitellinae*, which normally accepts phenolglucosides (see above), rejects completely *S. triandra* L., which has both a high total concentration in phenolglucosides and a high content of the unusual salidroside (Tahvanainen *et al.* 1985b).

Tahvanainen *et al.* (1985b) show that in the laboratory *Plagiodera versicolora* Laich. adults prefer leaves of willows with moderate to low phenolglucoside content. This contradicts the results from Soetens *et al.* (1991) (see below). It is possible that the Finnish population studied by Tahvanainen *et al.* (1985b) and the Belgian population studied by Soetens *et al.* (1991) have different food preferences, as demonstrated for geographically separated populations of another leaf beetle species, *Phratora vitellinae* (Rowell-Rahier 1984c). Additionally, conflicting results might be at least partially explained by confounding factors, such as leaf nutritional value or alternative chemical and mechanical defences, which were not taken into account when establishing the correlations.

Leaf pilosity is another efficient defence against herbivorous insects. High leaf pilosity reduces the nutritional value of a given amount of ingested food and a dense coverage of trichomes is an efficient mechanical barrier for small insects nibbling at the surfaces of leaves. Young larvae of *Phratora vitellinae* are only able to feed on the undersurface of the leaves of *S. caprea*, if the leaves have been shaved (Rowell-Rahier & Pasteels 1982). The related species *Phratora vulgatissima*, however, is able to circumvent this barrier, and cuts the trichomes before feeding on the undersurface of *S. viminalis* leaves (unpublished results).

Phenolics as positive cues for specialised insects

Insect specialists are not only able to tolerate and detoxify plant chemical defences; some additionally utilise plant secondary metabolites as feeding and oviposition stimulants.

In a field study involving two beetle species (*Phratora vitellinae* and *Plagiodera versicolora*), as well as a common sawfly (*Pontania proxima* (Lepeletier)), the correlation between herbivore abundance and amount of salicin and salicortin in leaves of individual *S. alba* (poor in phenolglucosides), *S. fragilis* (rich in phenolglucosides), and several of their hybrids containing intermediate level of phenolglucosides was tested. The results show that phenolglucosides have no significant effect on the distribution of *Phratora vitellinae* adults and *Plagiodera versicolora* larvae, but the phenolglucosides may partly explain (via a positive correlation) the observed variation in the distribution of *Phratora vitellinae* larvae, *Plagiodera versicolora* adults, and *Pontania proxima* galls. Trichome abundance, however, might also explain (via a negative correlation) the distribution of those insects and it is not clear if the insects avoid trichomes or are stimulated by phenolglucosides (Rowell-Rahier *et al.* 1987; Soetens *et al.* 1991).

Feeding preferences for Salicaceae rich in phenolglucosides support the hypothesis that these compounds have a stimulatory effect on feeding, but are by no means a definite proof of it. For example, *Phratora vitellinae* feeds preferentially on willows rich in salicortin and salicin (Rowell-Rahier 1984b,c; Tahvanainen *et al.* 1985b; Soetens *et al.* 1991), but those willows are usually glabrous; the ability of this species to feed and develop on leaves of hairy willows poor in phenolglucosides after they have been shaved demonstrates that the phenolglucosides are not obligatory phagostimulants (Rowell-Rahier & Pasteels 1982). However, Tahvanainen *et al.* (1985b) reported that this leaf beetle species prefers to feed on agar-based food containing a concentration of up to 1% salicin.

So far phagostimulation by phenolics has been demonstrated clearly only for a few leaf beetle species. First, the flavonoid luteolin-7-glucoside, and the phenolglucosides salicin and populin act as feeding stimulants for *Chrysomela vigintipunctata costella* (Marseul) and *Plagiodera versicolora distinctata* Baly. For a third species, *Lochmaea capreae cribata*, luteolin-7-glucoside only is active (Matsuda & Matsuo 1985). These species nibble at pieces of filter paper impregnated with solutions of those phenolics, especially in combination with sucrose, but populin is able to stimulate feeding of *Chrysomela vigintipunctata costella* in the absence of sucrose.

Secondly, the relationship between intraspecific variation in phenolglucosides in individual trees of *S. lasiolepis* and the damage due to herbivory by the leaf beetle *Chrysomela aenicollis* (Schaeffer), was established by Smiley *et al.* (1985) in California. The level of herbivory is positively correlated with the level of phenolglucosides in leaves. Both larvae and adults of *Chrysomela aenicollis* prefer the phenolglucoside-rich willow *S. orestera* to the phenolglucoside-poor *S. lutea* Nutt in feeding choice tests. Moreover, salicin itself stimulates feeding by adults in conjunction with sucrose (Rank, in preparation). Interestingly, the ovipositing female shows no preference for either species of willow. The results of these laboratory tests are confirmed by the distribution of the adults and egg batches in nature on four willow species representing a gradient of phenolglucoside content. Feeding preference,

rather than oviposition preference, determines host selection by this beetle (Rank, in preparation).

So far, the evidence suggesting that salicaceous phenolics could act as oviposition stimulants for specialised insects is only suggestive, and definitive proof is still lacking. Roininen and Tahvanainen (1989) show that the host plant spectra of two species of sawflies (*Nematus salicis* L. and *Nematus pavidus* Lepeletier) is determined by the behaviour of ovipositing females rather than by larval performance. In the specialised species *Nematus salicis*, the match between oviposition and larval growth and survival is better than in the more polyphagous species *Nematus pavidus*. For both species, however, there is a clear correlation between larval performance and total phenolglucosides (but not with total phenolics). The oligophagous *Nematus salicis* does better on tissue with moderate phenolglucoside content, whereas the polyphagous *Nematus pavidus* performs best on tissue with low phenolglucoside content. *Nematus salicis* prefers *S. fragilis* and *S. pentandra* L. for oviposition and both species have rather similar and otherwise unique compositions of phenolglucosides compared to the other species offered in the multiple choice tests (Roininen & Tahvanainen 1989).

Rowell-Rahier (1984b) reported that in the field the proportion of *Phratora vitellinae* observed in copulation was higher on *S. nigricans*, which has leaves rich in phenolglucosides, than on *S. cinerea*, whose leaves lack phenolglucosides. Further experiments are necessary to show a direct influence of the host plant on the sexual behaviour of the beetles.

Phenolglucosides as precursors of insect defence

A further step in the adaptation of insects to their host-plant is the utilisation of the phytotoxins for their own benefit. For example, the larvae of all Chrysomelina and *Phratora* (Phyllodectina) are protected by a secretion oozing from exsertile glands. In most species, the defensive secretions contain various iridoid monoterpenes. However, some species do not produce these monoterpenes, but instead make aromatic compounds such as salicylaldehyde (Pasteels *et al.* 1984). The *de novo* synthesis of iridoid monoterpenes in at least seven different genera is the plesiomorphic condition in the evolution of the defensive secretions by leaf beetle larvae, and the production of aromatic compounds is a derived condition which can be explained by host plant influence (Pasteels *et al.* 1988). Salicylaldehyde, for example, is clearly derived from salicin. The utilisation of phenolglucosides as precursors of salicylaldehyde in the larval defensive secretion of some species of *Chrysomela* and *Phratora* is now well documented and was definitively demonstrated by feeding the larvae with radioactive salicin (Pasteels *et al.* 1983).

An important consequence of the utilisation of salicin is that the glucose produced by the hydrolysis of salicin is recovered and salicin thus becomes a nutrient. It has been demonstrated that this added bonus can indeed have a significant impact on larval growth. The secretion was collected daily in larvae from species producing either *de novo* toxins, or plant-derived toxins, and the resulting adults were weighed. Their weight was compared to that of control adults obtained from larvae of the same species in which the secretion was not removed. In the species producing autogenous iridoids, the adults weighed significantly less than those resulting from the larvae in which the secretion was not renewed, demonstrating that the synthesis of the

defensive compounds is indeed costly. In *Phratora vitellinae*, which makes salicylaldehyde from the host plant salicin, the adults in contrast weighed more than the controls when their salicylaldehyde secretion was removed daily, presumably as a result of the extra glucose they acquired during the repeated breakdown of salicin (Rowell-Rahier & Pasteels 1986). Evidence suggests that the two enzymes necessary to derive salicylaldehyde from salicin, a β-glucosidase and an oxidase, are also involved in the final steps of the biosynthesis of iridoids in related species. Only small changes in the specificity of these enzymes, especially of the oxidase, are required for switching from *de novo* defence to plant-derived defence, with no additional metabolic cost (Pasteels *et al.* 1990). Thus an understanding of the proximate mechanisms involved in the utilisation of a plant precursor allows better insight into the ultimate cause of the evolution of this trait (Pasteels & Rowell-Rahier 1991).

At hatching the larvae are clustered and immobile on the leaf. An early defence would therefore seem to be critical. However, only those species secreting salicylaldehyde have functional glands on hatching. Species producing *de novo* secretion are not able to secrete at birth. Paradoxically then, only those larvae which depend on salicin normally found in their food seem to be able to produce a secretion before feeding. The obvious explanation is that the salicin is sequestered in the eggs and used as a precursor by the neonate larvae. This hypothesis has been confirmed experimentally; the eggs of some of the feeders on Salicaceae contain salicin, and these species are those whose larvae secrete salicylaldehyde. The adults do not sequester salicin for their own defence (they produce *de novo* isoxazolinone glycosides), but females are able to sequester salicin in their eggs for the benefit of both eggs and neonate larvae (Pasteels *et al.* 1986).

Phenolglucoside derivatives and the third trophic level

Salicin in the eggs is indeed a good protection, since it is toxic and a deterrent to predators such as ants at concentrations below those found in the eggs of the beetles (Pasteels *et al.* 1986). In the larvae too, salicylaldehyde is a useful chemical acting against predators (review in Pasteels *et al.* 1988). In the field, larvae of *Chrysomela aenicollis* survive better when they feed on *Salix* trees with leaves rich in salicin and are thus capable of producing large amount of salicylaldehyde in their defensive secretion (Smiley *et al.* 1985). However, some predators seem to specialise in larvae secreting salicylaldehyde. This was reported by Fabre (1891) for the wasp *Odynerus nidulator* Saus. The wasps were observed to repeatedly capture the larvae of *Chrysomela populi* L. on the same plant and to store exclusively this prey in their nest. In California, a predatory wasp, *Symmorphus* sp., also specialises in the larvae of *Chrysomela aenicollis*, and another specialised predator belonging to the Syrphidae shows no aversion to salicylaldehyde (Smiley & Rank 1986; Rank, in preparation). Salicylaldehyde often permeates the air around the willow shrubs which are infested by the larvae, and this aromatic compound should be a good olfactory cue for specialised predators. However, to our knowledge, this has not yet been tested.

The female of the sawfly *Tenthredo olivacea* Kl. feeds on larvae producing iridoid monoterpenes (e.g. *Plagiodera versicolora*), but also on larvae producing salicylaldehyde (e.g. *Phratora vitellinae*). In feeding choice experiments, this predator prefers to feed on prey previously encountered, and is reluctant to feed on prey which are met for the first time. This behaviour is independent of the species to which

the larvae belong and their type of chemical defence (Pasteels & Grégoire 1984). If widespread, such behaviour of predators will favour chemical diversity of defensive compounds in insects sharing the same habitat. Specialist predators and selective pressure for chemical diversity in defence could explain why the utilisation of phenolglucosides for defence does not occur in the larvae of all leaf beetle species feeding on the Salicaceae (e.g. *Plagiodera versicolora* and several *Phratora* species) even though, as argued above, this utilisation only requires small changes in existing enzymatic systems and is also energetically advantageous.

Conclusion: the evolution of the interactions between three trophic levels

The evolution of plant-herbivore-predator interactions is a dynamic process involving adaptations and counteradaptations at each trophic level. We have only an 'instantaneous' picture reflecting the status of the interaction at the present.

Phenolics are plant defensive compounds to which at least some herbivorous insects have adapted to the point of not only using them to find their host plant, but also using them to derive their own defensive toxins from them both cheaply and easily. However, some predators have coadapted too: they can circumvent the plant-derived defences used by the herbivores and possibly use them as cues to find their prey.

Within the last 20 years several hypotheses have been developed. They allow us to make predictions about the evolution of plant defence against herbivory and about the type of interactions which are likely to have evolved between these plants and the insects feeding on them. How well do the patterns of phenolic production in the different willow species fit those theories?

The most striking pattern in the defence of willows is the dichotomy between species relying on trichomes and leucoanthocyanidins, and species relying on phenolglucosides for leaf protection. These two different types of defence can tentatively be assigned respectively to the 'quantitative' and the 'qualitative' defences described by Feeny (1976). Trichomes and leucoanthocyanidins probably act mainly as digestibility reducers, whereas phenolglucosides and their derivatives seem to have specific toxic and deterrent effects.

Feeny (1976) and Rhoades and Cates (1976) predicted that plants protected by qualitative defences should be eaten mostly by specialised insects which are able to detoxify the defensive compounds present in the leaves. In consequence, qualitative defence are likely to be strongly diversified. Both these predictions are confirmed, if the phenolglucosides present in the leaves of some willow species are classified as 'qualitative' defence against herbivory. Firstly, the phenolglucosides have diverse and different structures in different willow species. Secondly, in a bibliographical survey, Rowell-Rahier (1984a), using a British fauna for the moths, a French one for the weevils, and a German one for the sawflies, shows that the presence or absence of phenolglucosides (or alternatively the absence or presence of leucoanthocyanidins) in *Salix* leaves is related to the degree of dietary specialisation of the insects feeding on these leaves. The results show that *Salix* species with phenolglucosides tend to be eaten by specialised herbivores and avoided by generalists. Conversely, *Salix* species without phenolglucosides tend to be the food of more polyphagous insects and tend to be avoided by the more specialised ones. Of course, there are exceptions to this

rule. *Phratora vulgatissima*, for example, is specialised on hairy willows and is able to circumvent this defence (see above).

The diversity of phenolglucosides could result from 'diffuse coevolution' (*sensu* Futuyma & Slatkin 1983) between willows and specialised herbivores or from 'sequential evolution' (*sensu* Jermy 1984). In the first case, it would be the specialised herbivores which act as the main selective pressure on the evolution of defensive chemistry in willow leaves. In the second case, other agents such as pathogens would provide the selective pressure and the specialised herbivorous insects adapt afterwards to the newly-evolved plant characteristics. For willows, the data presently available do not allow us to differentiate between these two evolutionary scenarios.

The apparency hypothesis (Feeny 1976) suggests that, for herbivores, plants with quantitative defences should be more predictable in space and time than those with qualitative ones. There is no evidence that this prediction is true for willows.

However, the 'resource allocation theory' (Coley *et al.* 1985) might provide more insights into the evolution of protective strategies in willows. According to these authors, plants living in favourable conditions are able to compensate for herbivory by fast growth and regeneration and should therefore opt for the least expensive form of defence available. Moreover, the theory predicts that carbohydrate-based defence, e.g. phenolics, should increase when carbon/nutrient balance is in favour of a carbohydrate resource (Bryant *et al.* 1983). Experimental data described above (Larsson *et al.* 1986; Bryant 1987; Price *et al.* 1989) are in agreement with this prediction.

Willows characterised by leaves with abundant trichomes and leucoanthocyanidins very probably invest proportionately more in defence than willows characterised by the presence of phenolglucosides in their leaves. Therefore, the resource allocation theory would support the hypothesis that willow species naturally occurring in less favourable conditions should have trichomes and leucoanthocyanidins rather than phenolglucosides.

Finally, the presence of phenolglucosides in both genera of the Salicaceae, *Salix* and *Populus*, as well as an independently-derived phylogenetic hypothesis (Scharfetter 1953), suggests that the defence type exemplified by glabrous leaves rich in phenolglucosides is the plesiomorphic condition in willows. Of course, it remains to be shown if the secondary defensive strategy (trichomes) has evolved as the result of the selective pressure applied by specialised herbivorous insects or as a response to different growing conditions.

Many ideas developed in this section are of a very speculative nature and we hope that they will stimulate further discussion and exchange of ideas.

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